Soil and Plant Minerals Associated with Rice Straighthead Disorder Induced by Arsenic

WenGui Yan,* Hesham A. Agrama, Nathan A. Slaton, and James W. Gibbons

Rice

ABSTRACT

Application of As as monosodium methanearsonate (MSMA) to soil has become the common practice for rice (*Oryza Sativa* L.) straighthead evaluation, a physiological disorder. So far, no study has reported on soil mineral availability and plant mineral uptake as affected by MSMA. Understanding how MSMA influences the availability and uptake should help reveal the causal factors of straighthead. Six cultivars rated as resistant (3), susceptible (2), and moderately susceptible (1) to straighthead were studied in soils receiving 0 and 6.7 kg MSMA ha^{-1} in 2004 and 2005. Soil, flag leaves, and heading panicles were sampled and analyzed. Straighthead induced by MSMA was so severe that the susceptible cultivars yielded no grain, which validated the study. MSMA incorporation decreased soil pH, P, Mg, and Ca, increased As, S, and Mn, but had no influence on soil EC, Na, K, Zn, Cu, Fe, and organic matter. Decreased soil pH resulting from the MSMA was associated with less Ca, Mg, and P but more S, Mn, and As in the soil. MSMA increased As, Cu, Mn, Fe, S, and K but decreased B contents in the flag leaves, and increased As, Mn, S, K, and P but decreased Zn and Ca contents in the panicles. Straighthead reduced grain yield and was associated with decreased Ca, Mn, and S, but not with As in flag leaves. Comparisons between reported naturally occurring straighthead and the artificially induced one from this study indicate plant and soil nutrients may behave differently when MSMA is applied.

Rice was domesticated in northeastern India and southern China about 8000 yr ago and is the staple food for more than 50% of the world's population (Khush, 1997). Straighthead, a physiological disorder that causes grain sterility in rice, was first reported in the United States in 1912 (Wells and Gilmour, 1977) and can cause complete yield loss when severe (Yan et al., 2005). Other reports of straighthead followed in Japan (Iwamoto, 1969), Australia (Dunn et al., 2006), Portugal (called 'branca') (Cunha and Baptista, 1958), and Thailand (Weerapat, 1979). Since the 1940s, a water management practice has been used to prevent straighthead by draining water about 2 wk after permanent flooding, drying the soil until rice leaves exhibit drought stress symptoms, and resuming the flooding (Todd and Beachell, 1954; Rasamivelona et al., 1995; Slaton et al., 2000; Yan et al., 2005). Draining and drying may stress rice plants and limit yield potential, waste water, and increase irrigation expenses.

Soil aeration is believed to speed the decay of soil organic matter (Anonymous, 1946) and help oxidize As into arsenate, which is biologically inactive (Marin et al., 1992). Arsenic is toxic to many plant species including snap bean (*Phaseolus vulgaris* L.) (Sachs and Michael, 1971), soybean [*Glycine max* (L.) Merr.], potato (*Solanum tuberosum* L.), cotton (*Gossypium hirsutum* L.), and rice (Baker et al., 1976). Because the symptoms of As injury are similar to straighthead of rice, incorporation of As as MSMA has become the common practice for evaluating rice susceptibility to straighthead in breeding programs (Horton et al., 1983; Frans et al., 1988; Dunn et al., 2006; Slaton et al., 2000; Wilson et al., 2001; R.H. Dilday et al., unpublished data, 1984). No study has investigated the influence of MSMA on soil mineral availability and nutrient uptake by rice, although three investigations have been reported on soil and plant minerals associated with naturally occurring straighthead (Iwamoto, 1969; Dunn et al., 2006; Belefant-Miller and Beaty, 2007). The occurrence and severity of straighthead have been associated with soil organic matter (Anonymous, 1946), low pH and low free iron (Baba and Harada, 1954), thiol compounds (Iwamoto, 1969), sandy to silt loam soil textures (Rasamivelona et al., 1995; Slaton et al., 2000), continuous flooding (Wilson et al., 2001), high soil As (Gilmour and Wells, 1980), N fertilization (R.H. Dilday et al., unpublished data, 1984; Dunn et al., 2006), and soil Cu availability (Ricardo and Cunha, 1968), but the exact causal factors of naturally occurring straighthead are still unknown. The most recent work suggested possible roles of magnesium but not As in naturally occurring straighthead by chemical analyses of rice plant (node, internode, stem, leaf, and root) and seed (brown and milled seed and hull) (Belefant-Miller and Beaty, 2007). Our research objective was to investigate the changes of soil and plant minerals and the association of these changes with straighthead induced by incorporation of As as MSMA. The goal of this investigation was to improve our understanding of soil and plant nutrient status and response to straighthead as an aid to help identify factors that contribute to this disorder.

W. Yan, USDA-ARS, Dale Bumpers Natl. Rice Res. Cent., 2890 Hwy. 130 East, Stuttgart, AR 72160; H. Agrama and J.W. Gibbons, Rice Res. and Ext. Cent., Univ. of Arkansas, 2900 Hwy. 130 East, Stuttgart, AR 72160; N.A. Slaton, Dep. of Crop, Soil, and Environ. Sci., Univ. of Arkansas, 1366 W. Altheimer Dr., Fayetteville, AR 72704. Received 4 Apr. 2008. *Corresponding author (Wengui.Yan@ars.usda.gov).

Published in Agron. J. 100:1655–1661 (2008).
doi:10.2134/agronj2008.0108

AJ AGRONOMY JOURNAL 1908–2008

Abbreviations: EC, electrical conductivity; MSMA, monosodium methanearsonate.

Table 1. Analysis of soil properties and minerals for soil samples before applying 6.7 kg ha^{-1} monosodium methanearsonate (MSMA) (before MSMA), after applying MSMA (after MSMA) in straighthead test area, and the field that never received MSMA application (no MSMA) in 2004 and 2005.

	pH	EC†	P	K	Ca	Mg	S	Na	Fe	Mn	Zn	Cu	As	SOM‡
		Umhos cm^{-1}	mg kg^{-1}											g kg^{-1}
No MSMA	5.9a§	188a	31a	180a	1053a	185a	9b	66a	312a	178b	0.9a	1.1a	5.9c	21a
Before MSMA	5.3b	196a	19b	182a	795b	154b	16a	70a	283b	211a	0.8b	1.2a	16.0b	22a
After MSMA	5.3b	192a	14b	164a	759b	146b	17a	74a	301ab	211a	0.8b	1.2a	19.5a	24a
CV, %	4	20	37	17	6	9	13	23	11	7	21	7	13	12

† EC, soil electrical conductivity.

‡ SOM, soil organic matter.

§ Means in each column with the same letter are not significantly different at the 0.05 probability level.

MATERIALS AND METHODS

Six rice cultivars were studied in a completely randomized split-plot design experiment with four replications in 2004 and 2005. Cultivar reaction or susceptibility to straighthead was rated as resistant ('Zhe 733' [Yan and Cai, 1991], 'Zao 402', and 'Luhongzao' [Yan et al., 2005] all from China), moderately susceptible ('Priscilla' [Rood, 1999], United States], and very susceptible ('Cocodrie' [Linscombe et al., 2000] and 'Mars' [Johnston et al., 1979], United States). Two fields near Stuttgart, AR, that had different As contents served as main plots each year. One field had received As in the form of MSMA at 6.7 kg MSMA ha^{-1} in alternating years and the other field had no known history of As application (No MSMA). Both fields were planted with commercial soybeans in the previous year of the study and prepared with Northwest tiller (Yakima, WA) for seeding. Subplots were the cultivars and each plot contained six rows with 0.3-m spacing between rows that were 1.5-m long. Each row was drill-seeded (Hege 1000 drill) with 3 g of rice, which is equivalent to a seeding rate of 65 kg ha^{-1} or 340 seeds m^{-2} as recommended (Slaton and Cartwright, 2001). The seeding at a depth of 2 cm was conducted on 21 May 2004 and 5 May 2005. In the MSMA field, 10 composite soil samples (0–10 cm) were collected from the entire test area before MSMA was applied each year (Before MSMA). Following collection of soil samples, 6.7 kg MSMA ha^{-1} was applied in a spray volume of 85 L ha^{-1} with a calibrated CO_2–backpack sprayer, and 10 more composite soil samples were collected before rice was drill-seeded (After MSMA). In the No MSMA field, 10 soil samples were collected after tillage. Regular weed control, consistent flood and fertilization at 135 kg ha^{-1} of N followed the description by Yan et al. (2005). The soil in all fields was classified as a Dewitt silt loam (fine, smectitic, thermic Typic Albaqualf).

Soil samples were ovendried at 50°C for 48 h to remove moisture and crushed to pass through a 2-mm sieve. Soil pH and electrical conductivity (EC) were determined on a 1:2 soil weight:water volume suspension with a glass electrode. Plant available nutrient indices were evaluated by extracting soil with Mehlich 3 solution (Mehlich, 1984). Nutrient composition of Mehlich 3 extracts was determined by inductively coupled plasma atomic emission spectrometry (ICP–AES). Soil organic matter content was determined by weight loss on ignition (Schulte and Hopkins, 1996). Total recoverable soil As was determined using the EPA 3050B digestion procedure (USEPA, 1996) and analyzed by ICP–AES.

The R3 growth stage or date of 50% heading was recorded for each plot based on a visual estimation when one-half of the panicles had emerged from the rice culms (Counce et al., 2000). When each cultivar reached 50% heading, flag leaves were collected in 2004 and 2005 and heading panicles were collected in 2005 only from 10 plants located near the center of each plot. The plant samples were placed in paper bags, dried for 2 d at 40°C, ground to pass through a 2-mm sieve, digested with HNO_3 and 30% H_2O_2 (Jones and Case, 1990) and the elemental (P, K, Ca, Mg, Na, S, Fe, Mn, Zn, Cu, and B) composition of digests was determined by ICP–AES at the University of Arkansas. Plant digests were later analyzed for As using inductively coupled plasma mass spectrometry (ICP–MS) at the University of Georgia, Athens, GA.

At maturity of growth stage R9, straighthead was rated using a 1 to 9 rating scale, 1 = not any symptoms of straighthead and 9 = the most severe straighthead as described by Yan et al. (2005). Plant height was measured from the soil surface to the tip of the upright panicle, and grain yield was measured by harvesting a 0.9-m length of the three center rows in each plot.

Statistical analyses were performed using SAS 9.1.3 (SAS Institute, Cary, NC). All correlation analyses were conducted using the CORR procedure. Means separation of the leaf data was conducted using the GLIMMIX procedure within a split-plot completely randomized design. The MSMA (whole plot) and cultivar (subplot) treatments are both considered fixed effects; the field assigned to each MSMA treatment is the random effect. Estimated means and their differences were calculated using the LSMEANS option with P-value adjustment for multiple comparisons via Tukey's HSD. Means separation of the panicle data was also conducted using the GLIMMIX procedure, although within a nested completely randomized design because only 1 yr of data was available (no MSMA treatment replication available). The cultivar within MSMA treatment is a fixed effect. Estimated means and their differences were again calculated using the LSMEANS option with P-value adjustment for multiple comparisons via Tukey's HSD. Soil chemical property data are presented as descriptive means and coefficient of variation (%CV) in Table 1. These mean calculations were performed in Microsoft Excel. Data were interpreted as significant when $P < 0.05$.

RESULTS

Soil Parameters Affected by MSMA

Mehlich 3 extractable soil K and Na were not different between years and MSMA treatments. Likewise, Mehlich 3 extractable soil P, K, Ca, and Na and soil pH, As (USEPA Method 3050), and soil organic matter were not different between years. Soil EC and Mehlich 3 extractable Zn and Fe were affected only by year. Annual changes in EC are normal as the amount of soluble salts present in topsoil fluctuates across time. Mehlich 3 soil Zn concentrations are considered very

Table 2. Variance analysis of minerals in flag leaves, days from seedling emergence to 50% heading, plant height, straighthead rating, and grain yield among rice cultivars grown in MSMA treated (6.7 kg ha^{-1}) and untreated soils in 2004 and 2005, and heading panicles in 2005.

		F value in variance analysis															
Source	df	Heading	Plant height	Straight-head	Grain yield	P	K	Ca	Mg	S	Na	Fe	Mn	Zn	Cu	B	As
		d	cm	rate	kg ha^{-1}	mg kg^{-1}											
Flag leaves																	
Cultivar	5	292***	13***	165***	127***	4*	<1	28***	25***	52***	17***	4***	25***	3*	21***	5**	14***
MSMA	1	1	12***	471***	19***	<1	36***	1	<1	15***	<1	<1	28***	1	7***	<1	19***
Cultivar × MSMA	5	2	2	165***	52***	1	2	5***	2	4**	5***	2	4**	1	8***	<1	1
Heading panicles																	
Cultivar (MSMA)	9	172***	3*	271***	42***	2	5***	27***	<1	1	5***	4**	8***	1	6**	4**	13***

* Significantly different at the 0.05 probability level.

** Significantly different at the 0.01 probability level.

*** Significantly different at the 0.001 probability level.

low (Table 1), but because soil pH is somewhat acidic (<6.0) it would not be expected to adversely influence rice growth and yield (Slaton et al., 2002). Soil pH averaged 5.9 in the No MSMA soil, which was greater than soil that received MSMA (5.3). Soil pH was not different before and after MSMA application in the straighthead test soil. Mehlich 3 extractable P and recoverable As were affected only by MSMA treatment. Plant available soil P was greater in the No MSMA soil compared with soil that received MSMA, but would not be expected to limit the growth and yield of flood-irrigated rice (Slaton et al., 2006). Although Mehlich 3 extractable Mn was affected by both year and MSMA treatment, its concentration in the soil was considered above optimum for rice. Soil recoverable As increased 3.5 mg kg^{-1} after MSMA application to the straighthead test soil (Before MSMA), which contained 10.1 mg kg^{-1} more As than the No MSMA soil.

Significant correlations were identified between soil parameters among the three soils, No MSMA, Before, and After MSMA treated soils. Soil pH was positively correlated with Ca (r = 0.92), Mg (r = 0.78), and P (r = 0.41), but negatively correlated with As (r = -0.87), S (r = −0.73) and Mn (r = -0.59). Arsenic was correlated positively with S (r = 0.78) and Mn (r = 0.58), but negatively with Ca (r = −0.90), Mg (r = −0.66) and P (r = −0.58). Ca was correlated positively with Mg (r = 0.87) and P (r = 0.52) and negatively with S (r = −0.73) and Mn (r = −0.71). Sulfur was correlated positively with soil organic matter (r = 0.53), Mn (r = 0.46), and Cu (r = 0.36), and negatively with P (r = −0.74) and Mg (r = −0.38). Magnesium was negatively correlated with Mn (r = −0.72), Fe (r = −0.51), EC (r = −0.39), and Zn (r = −0.38). Phosphorus was correlated positively with K (r = 0.64), EC (r = 0.51), and Zn (r = 0.46) and negatively with soil organic matter (r = −0.43), Mn (r = −0.40), and Cu (r = −0.40).

Leaf and Panicle Parameters Affected by MSMA

Chemical analysis for productive tissues was strongly suggested by the elemental concentrations of flag leaves in 2004, so heading panicles were collected in 2005 since susceptible cultivars set no seeds at all in addition to leaf collection. The six cultivars differed significantly in days to 50% heading, plant height, straighthead rating and grain yield as well as all the elemental concentrations in flag leaves and panicles, except K (Table 2). Cultivar significantly influenced the flag leaf concentrations of S, followed by Ca, Mg, Mn, Cu, Na, As, B, P, Fe, and Zn, and similarly in the heading panicles Ca had the most differences, followed by As, Mn, Cu, K, Na, Fe, and B. Application of MSMA to the soil affected straighthead rating, grain yield, and plant height as well as K, S, Mn, Cu, and As, but 50% heading, P, Ca, Mg, Na, Fe, Zn, and B were not affected in the flag leaves. K was mostly affected by the MSMA incorporation, followed by Mn, As, S, and Cu in the flag leaves.

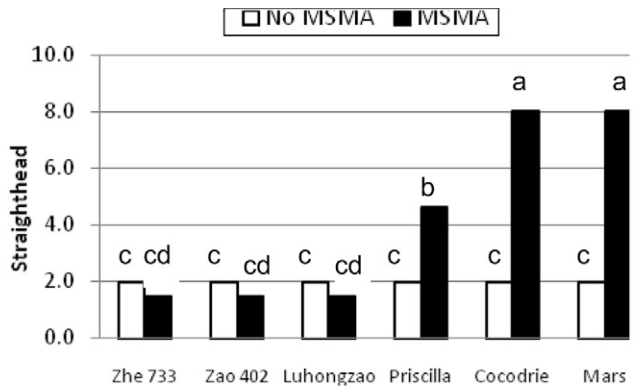
Significant correlations were observed between these characteristics, including the minerals in the flag leaves. Straighthead was correlated negatively with grain yield (r = −0.89), plant height (r = −0.60) and flag leaf contents of Ca (r = −0.51), Mn (r = −0.31) and S (r = −0.26) and positively with days to head. Leaf Ca was associated positively with grain yield (r = 0.60), leaf Mn (r = 0.81), Fe (r = 0.42), S (r = 0.40), and Cu (r = 0.38) and negatively with days to 50% heading (r = −0.64). The increased Mn in the flag leaves was associated with the increased leaf Ca, Fe (r = 0.49), Cu (r = 0.48), S (r = 0.40), and As (r = 0.29), but with the decreased days to 50% head (r = −0.56). Flag leaf S concentration was correlated positively with plant height (r = 0.37), grain yield (r = 0.35), and leaf P (r = 0.59), K (r = 0.49), and Mn (r = 0.40) and negatively with days to head (r = −0.64) and leaf Na (r = −0.41) and Zn (r = -0.41). Leaf As concentration was correlated positively with the leaf Cu (r = 0.65), Na (r = 0.58), Fe (r = 0.51), and Mn (r = 0.29), but negatively with leaf K (r = −0.49) and B (r = −0.42).

Differential Response of Cultivar to MSMA on Leaf and Panicle Parameters

Cultivars responded differently to the MSMA incorporation on straighthead, grain yield, and leaf Ca, S, Na, Mn, and Cu concentrations and panicle K, Ca, Na, Fe, Mn, Cu, B, and As concentrations (Table 2). Straighthead induced by the MSMA treatment was so severe for the susceptible cultivars, Cocodrie and Mars, that their grain yields were completely lost (Fig. 1). This indicated a successful induction of straighthead for the study. In contrast, straighthead-resistant cultivars, Zhe 733, Zao 402, and Luhongzao, showed no straighthead symptoms without grain-yield differences between the MSMA treatments. The effect of MSMA treatment on Priscilla, rated as moderately susceptible, was intermediate for the symptoms and resulting yield reduction (Fig. 1). Leaf Ca concentrations decreased for Cocodrie and Priscilla, and increased for

Mars but were not different for the three resistant cultivars when MSMA was applied. However, panicle Ca concentrations decreased the most for Zhe733 and were not different for Cocodrie, Zao402, and Luhongzao up to the MSMA treatment. Flag leaf Mn concentrations increased in the three resistant cultivars, but decreased in susceptible cultivar Mars. Panicle Mn increased in Cocodrie, Priscilla, and Zhe 733 but decreased in Luhongzao in response to MSMA application (Fig. 2). In response to the MSMA, Na concentrations decreased for Mars only in flag leaf, but increased for Zao 402 in panicle. Flag leaf Cu concentrations also varied among cultivars in response to MSMA, but maximal differences were generally <1 mg kg^{-1} with no clear trend exhibited among straighthead susceptible and resistant cultivars. Similarly, leaf S concentration was increased after MSMA application for resistant cultivar Lohongzao, intermediate Priscilla, and susceptible Cocodrie.

For rice panicles, MSMA application increased K in Zhe 733 and Cocodrie, Cu in Luhongzao, and Fe in three resistant



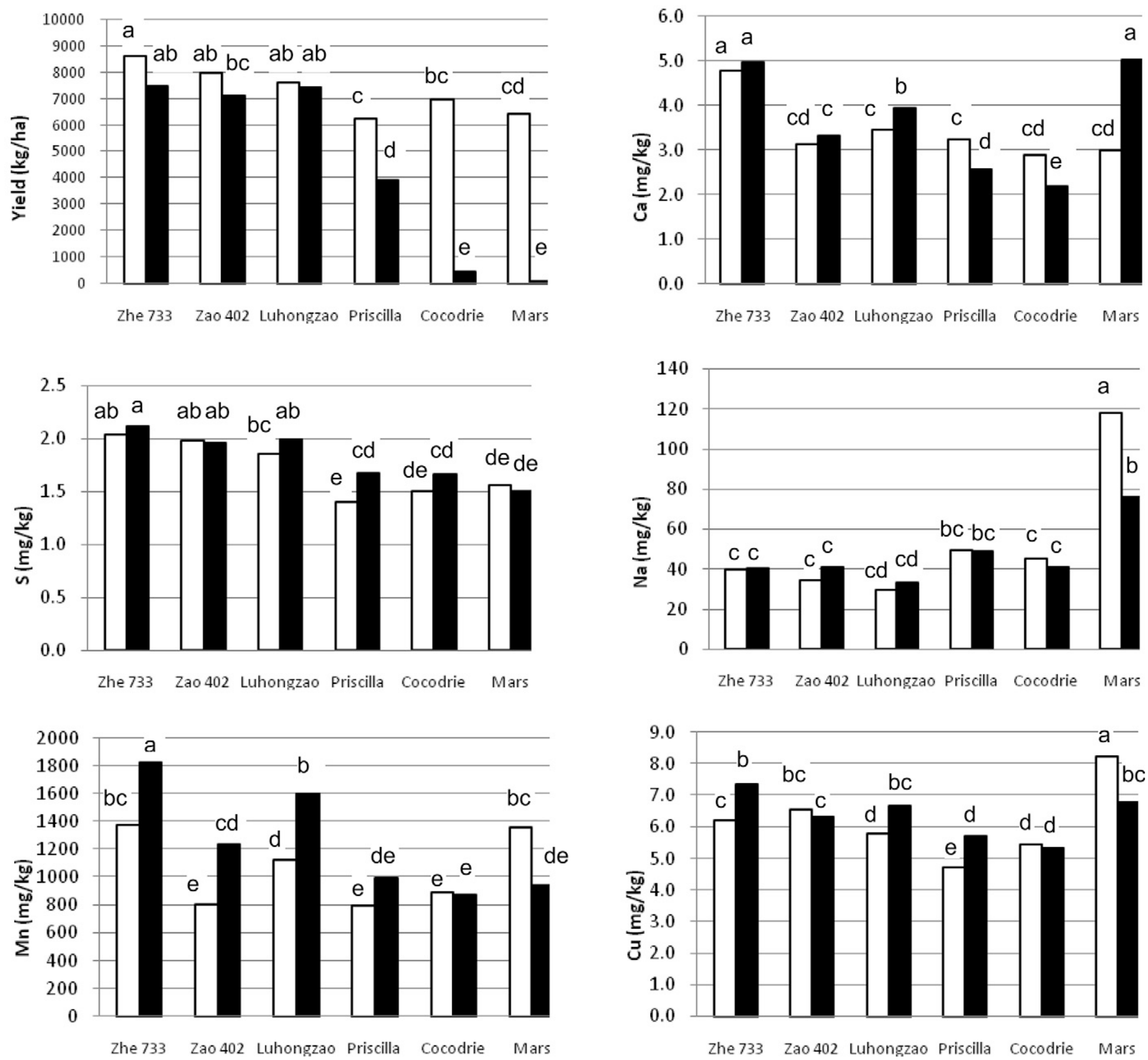


Fig. 1. Differential response of rice cultivars to soils treated with monosodium methanearsonate (MSMA) on straighthead ratings, grain yield, and mineral contents in flag leaves at 50% heading (Tukey-Kramer Grouping for cultivar least square means and LS-means with the same letter not significantly different at the 0.05 probability level).

cultivars (Fig. 2). MSMA application decreased B concentrations in panicles of Luhongzao. Panicle As concentrations decreased in Lunhongzao and Zao 402, increased in panicles of Priscilla and Cocodrie, and remained constant in Zhe 733.

DISCUSSION

The physiological disorder straighthead has been associated with a number of soil and crop management factors in studies and field observations (Baba and Harada, 1954; Dunn et al.,

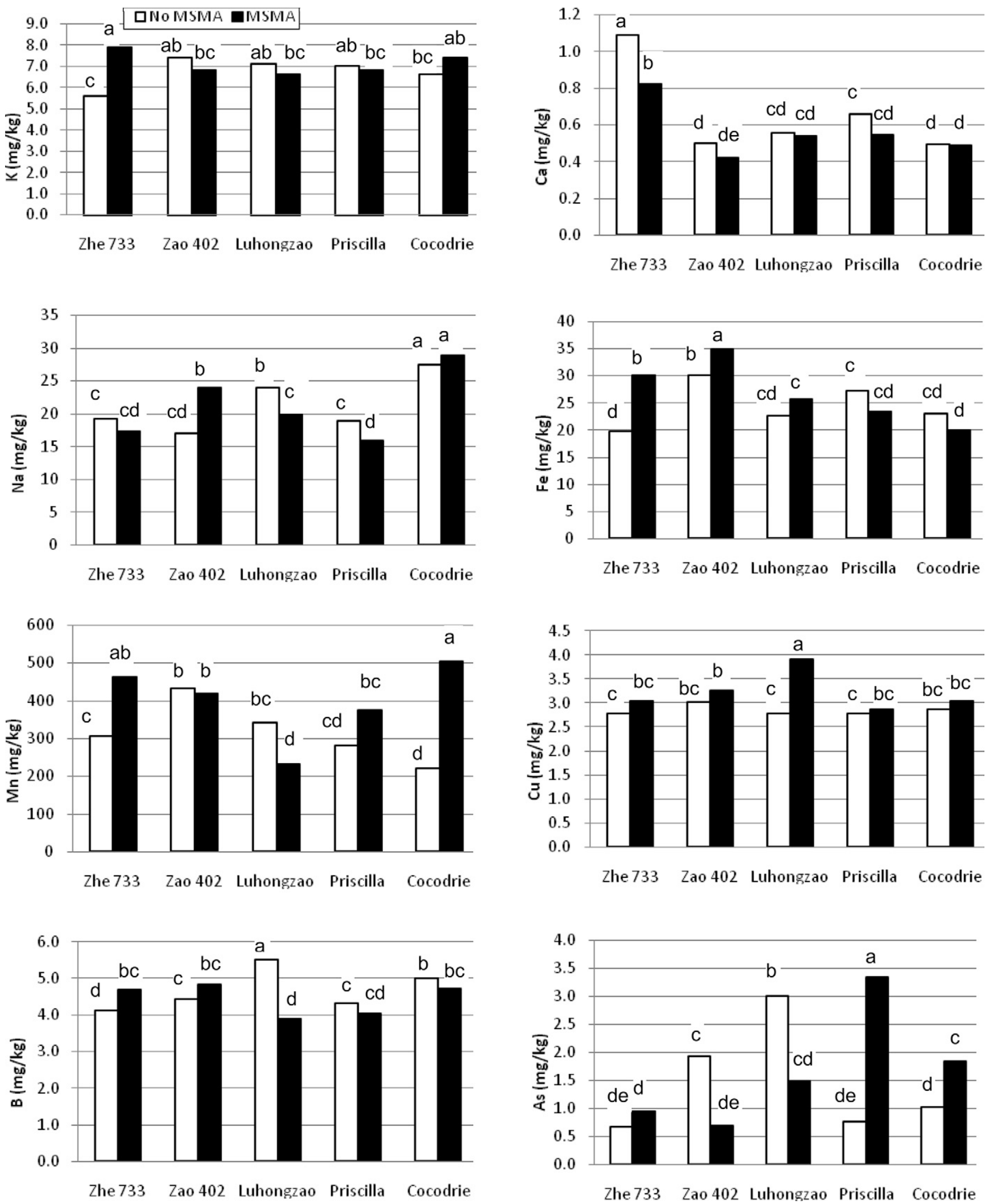


Fig. 2. Differential response of rice cultivars to soils treated with monosodium methanearsonate (MSMA) on mineral concentration in the panicles at 50% heading (Tukey-Kramer Grouping for cultivar least square means and LS-means with the same letter not significantly different at the 0.05 probability level).

2006; Anonymous, 1946; Gilmour and Wells, 1980; Iwamoto, 1969; Rasamivelona et al., 1995; Ricardo and Cunha, 1968; Slaton et al., 2000, Wilson et al., 2001), but its mechanism of reducing rice yield is unknown. Analyses of leaf and panicle tissue in this study showed that none of the essential elements appear low enough to be considered deficient or high enough to be considered toxic, based on our current understanding of critical concentrations of essential elements, i.e., total tissue concentration (Fig. 1 and 2). Furthermore, the differences between straighthead susceptible and tolerant and resistant cultivars were not consistent between two treatments of MSMA. As a result, yield loss in susceptible cultivars in response to MSMA application was not associated with the levels of essential nutrients in the study.

Cultivars showed different straighthead symptoms, severity ratings, and grain yields (Fig. 1) in response to MSMA application, which followed similar trends as those reported by Yan et al. (2005).

Evatt and Atkins (1957) were able to control straighthead by applying Feralum, a mixture of ferric and aluminum sulfates. Iwamoto (1969) reported that soils in Japan where straighthead occurs are acidic and deficient in Ca, Mg, Fe, and Mn. Belefant-Miller and Beaty (2007) reported that soil where rice exhibited straighthead contained lower Mehlich 3 soil Zn, Cu, Ca, Mg, and Mn concentrations as well as lower pH than soil where rice showed no straighthead. Our study showed soil receiving MSMA had lower soil pH, less Ca and Mg but more Mn than soil that had never received MSMA. Soil with no history of As application contained 5.9 mg As kg^{-1} (No MSMA) compared with 16 to 19.5 mg kg^{-1} in soil with a history of MSMA application. This does not agree with Belefant-Miller and Beaty (2007) who reported straighthead symptoms in a soil with As concentration as low as 4.5 mg kg^{-1}.

In Portugal, Cu deficiency was found to be associated with straighthead (Karim and Vlamis, 1962). Application of copper sulfate to the soil when seedlings are transplanted prevents or greatly reduces straighthead (Cunha and Baptista, 1958). Ricardo and Cunha (1968) concluded that copper sulfate acts simply as a supplier of Cu to the plant since soil organic matter may bind Cu, reducing its availability for uptake by plants. Soils that have high organic matter content are more prone to straighthead, especially when planted with susceptible cultivars. In contrast, Belefant-Miller and Beaty (2007) reported lower organic matter content in a soil with naturally occurring straighthead compared with soil where no straighthead was observed. Under the highly anaerobic soil conditions in flooded rice fields, solubility of Cu may be greatly reduced by H_2S. Marschner (1995) associated straighthead-like symptoms with Cu deficiency in wheat (*Triticum durum* L.). However, in our study, MSMA treatment had no influence on soil Cu and no correlation existed between flag leaf Cu and straighthead incidence. Furthermore, MSMA did not change soil organic matter in the present study.

Soil P decreased following MSMA application in this study, which has never been reported in soils where straighthead occurs naturally. In spite of these discrepancies, the association of straighthead with soil pH, Ca, and Mg is not different between the soils where straighthead naturally occurs and where it is artificially induced.

Iwamoto (1969) showed that rice exhibiting straighthead contained greater Ca and S concentrations, but less Fe, Mn, K, and P than plants showing no straighthead. Belefant-Miller and Beaty (2007) reported that stems of plants exhibiting naturally occurring straighthead had lower concentrations of S, K, Mg, Na, Zn, Fe, and Cu, but only Na and Mg concentrations were lower in plant leaves compared with plants showing no straighthead. Our study demonstrated that plants growing in MSMA treated soil contained more As, Cu, Mn, Fe, S, and K, but less B in flag leaves, and more As, Mn, S, K, and P, but less Zn and Ca in panicles than those growing in soil receiving no MSMA. Straighthead had a direct association with decreased concentrations of Ca, Mn, and S in flag leaves. Iron, S, and Cu had an indirect influence to straighthead via Ca. Similarly, Fe, Cu, S, and As indirectly affected straighthead via Mn. Phosphorus, K, Na, and Zn indirectly affected straighthead via S.

These discrepancies should be expected for the comparisons between naturally occurring straighthead in the literature and artificially induced straighthead in our study. Meanwhile, the discrepancies indicate the complexity of responsible factors to straighthead and raise more questions for further studies.

No matter what factors cause straighthead disorder or disease, the discovery of resistant germplasm can greatly enhance its control with genetic means. Molecular markers in various chromosomal regions have been identified to facilitate this effort (Agrama and Yan, unpublished data, 2008).

ACKNOWLEDGMENTS

The authors thank Paul Counce, Xueyan Sha, and Helen Belefant-Miller for critical review; Kathleen Yeater and Howard Black for statistical assistance; and Nancy Wolf, Tony Beaty, Rachel Joslin, Patricia Calvert, Edith Baugh, Emily Hendrix, and Tiffany Sookaserm for technical assistance.

REFERENCES

Anonymous. 1946. Symptoms of straighthead and its control. Rice J. 49(7):20–36.

Baba, I., and T. Harada. 1954. Akiochi, Akagare and straighthead. *In* Physiological diseases of rice plant in Japan. Ministry of Agric. and Forestry, Japanese Gov., Tokyo.

Baker, R.S., W.L. Barrentine, D.H. Bowman, W.L. Hawthorne, and J.V. Pettiet. 1976. Crop response and arsenic uptake following soil incorporation of MSMA. Weed Sci. 24:322–326.

Belefant-Miller, H.B., and T. Beaty. 2007. Distribution of arsenic and other minerals in rice plants affected by natural straighthead. Agron. J. 99:1675–1681.

Counce, P.A., T.C. Keisling, and A.J. Mitchell. 2000. A uniform, objective, and adaptive system for expressing rice development. Crop Sci. 40:436–443.

Cunha, J.M.A., and J.E. Baptista. 1958. Estudo da branca do arroz. I. Combated a doenca. Agron. Lusit. 20:17–64.

Dunn, B.W., G.D. Batten, T.S. Dunn, R. Subasinghe, and R.L. Williams. 2006. Nitrogen fertilizer alleviates the disorder straighthead in Australian rice. Aust. J. Exp. Agric. 46:1077–1083.

Evatt, N.S., and J.G. Atkins. 1957. Chemical control of straighthead in rice. Rice J. 60(5):26–37.

Frans, R., D. Horton, and L. Burdette. 1988. Influence of MSMA on straighthead, arsenic uptake and growth response in rice. Res. Ser. 302:1–12. Univ. of Arkansas, Agri. Exp. Sta., Fayetteville.

Gilmour, J.T., and B.R. Wells. 1980. Residual effects of MSMA on sterility in rice cultivars. Agron. J. 72:1066–1067.

Horton, D., R. Frans, and T. Cothren. 1983. MSMA-induced straighthead in rice (*Oryza sativa*) and effect upon metabolism and yield. Weed Sci. 31:648–651.

Iwamoto, R. 1969. Straighthead of rice plants effected by functional abnormality of thiol-compound metabolism. p. 62–80 *In* Memoirs of the Tokyo Univ. of Agric. XIII. Tokyo Univ., Japan.

Johnston, T.H., B.R. Wells, M.A. Marchetti, F.N. Lee, and S.E. Henry. 1979. Registration of Mars rice. Crop Sci. 19:743–744.

Jones, J.B., and V.W. Case. 1990. Sampling, handling, and analyzing plant tissue samples. p. 389–428. *In* R.L. Westerman (ed.) Soil testing and plant analysis. 3rd ed. SSSA Book Series 3. SSSA, Madison, WI.

Karim, A.Q.M.B., and J. Vlamis. 1962. Micronutrient deficiency symptoms of rice grown in nutrient culture solutions. Plant Soil 16:347–360.

Khush, G.S. 1997. Origin, dispersal, cultivation and variation of rice. Plant Mol. Biol. 35:25–34.

Linscombe, S.D., F. Jodari, P.K. Bollich, D.E. Groth, L.M. White, Q.R. Chu, R.T. Dunand, and D.E. Sanders. 2000. Registration of 'Cocodrie' rice. Crop Sci. 40:294.

Marin, A.R., P.H. Masscheleyn, and W.H. Patrick, Jr. 1992. The influence of chemical form and concentration of arsenic on rice growth and tissue arsenic concentration. Plant Soil 139:175–183.

Marschner, H. 1995. Mineral nutrition of higher plants. 2nd ed., Academic Press, London.

Mehlich, A. 1984. Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. Commun. Soil Sci. Plant Anal. 15:1409–1416.

Rasamivelona, A., K.A. Gravois, and R.H. Dilday. 1995. Heritability and genotype × environment interactions for straighthead in rice. Crop Sci. 35:1365–1368.

Ricardo, C.P.P., and J.M.A.E. Cunha. 1968. Study of branca: A physiological disease of rice II. Relation between the soil redox potential and the disease: Action of cupper sulfate. Agron. Lusit. 29(1):57–97.

Rood, M.A. 1999. Bred for the south– New varieties resist disease, raise yields. Rice J. 102(1):24–25.

Sachs, R.M., and J.L. Michael. 1971. Comparative phytotoxicity among four arsenical herbicides. Weed Sci. 19:558–564.

Schulte, E.E., and B.G. Hopkins. 1996. Estimation of soil organic matter by weight loss-on-ignition. p. 21–31. *In* F.R. Magdoff et al. (ed.) Soil organic matter: Analysis and interpretation. SSSA, Madison, WI.

Slaton, N.A., and R. Cartwright. 2001. Rice stand establishment. p. 21–28. *In* N.A. Slaton (ed.) Rice production handbook. MP192–10M–1-01RV. Univ. of Arkansas, Little Rock.

Slaton, N.A., C.E. Wilson, Jr., R.J. Norman, and R.E. DeLong. 2006. Correlation of soil pH and Mehlich-3 phosphorus with postflood rice phosphorus concentrations in Arkansas. Commun. Soil Sci. Plant Anal. 37:2819–2831.

Slaton, N.A., C.E. Wilson, Jr., R.J. Norman, and E.E. Gbur, Jr. 2002. Development of a critical Mehlich 3 soil zinc concentration for rice in Arkansas. Commun. Soil Sci. Plant Anal. 33:2759–2770.

Slaton, N.A., C.E. Wilson Jr., S. Ntamatungiro, R.J. Norman, and D.L. Boothe. 2000. Evaluation of new varieties to straighthead susceptibility. p. 313–317. *In* R.J. Norman et al. (ed.). B.R. Wells Rice Res. Studies 1999. Res. Ser. 476. Univ. of Arkansas, Agri. Exp. Sta., Fayetteville.

Todd, E.H., and H.M. Beachell. 1954. Straighthead of rice as influenced by varieties and irrigation practices. The Rice Journal 57(6):20–22.

USEPA. 1996. Method 3050B. Acid digestion of sediments, sludges, and soils Available at www.epa.gov/epaoswer/hazwaste/test/pdfs/3050b.pdf (cited 8 Feb. 2008; verified 11 Aug. 2008). USEPA, Washington, DC.

Weerapat, P. 1979. Straighthead disease of rice suspected in southern Thailand. IRRN 4(3):6–7.

Wells, B.R., and J.T. Gilmour. 1977. Sterility in rice cultivars as influenced by MSMA rate and water management. Agron. J. 69:451–454.

Wilson, C.E., Jr., N.A. Slaton, D.L. Frizzell, D.L. Boothe, S. Ntamatungiro, and R.J. Norman. 2001. Tolerance of new rice cultivars to straighthead. p. 428–436 *In*: R.J. Norman et al. (ed.). B.R. Wells Rice Res. Studies 2000. Res. Ser. 485. Univ. of Arkansas, Agri. Exp. Sta., Fayetteville.

Yan, W., and G. Cai. 1991. Zhe 733, a high-yielding blast (B1)-resistant, good quality indica rice from China. Int. Rice Res. Newsletter 16(6):14.

Yan, W., R.H. Dilday, T.H. Tai, J.W. Gibbons, R.W. McNew, and J.N. Rutger. 2005. Differential response of rice germplasm to straighthead induced by arsenic. Crop Sci. 45:1223–1228.